EFFECT OF TEMPERATURE UPON SHELL MOVEMENTS OF CLAMS, VENUS MERCENARIA (L.) [1]

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Introduction

Knowledge of the effect of temperature on the physiological activities of mollusks is essential to the solution of many problems of shell-fisheries. Galtsoff (1928), in his studies of the effect of temperature on oysters, demonstrated its bearing on the problems of oyster culture and sanitary control of the oyster industry. His studies and those of Nelson (1921) and Hopkins (1931) added greatly to our knowledge of this phenomenon in relation to oysters, but little or nothing is known about other Pelecypoda. This study deals with the effect of temperature upon the shell movements of the hard-shell clam (*Venus mercenaria* L.).

In Pelecypoda, respiration and feeding are influenced by three factors, namely, the rate of activity of cilia of the gill epithelium, changes in size of the ostia, and by the movements of the shell-valves. It has already been shown (Galtsoff, 1928) that low temperatures induce hibernation in oysters. During the hibernation period the animal is unable to feed because of the disturbances of the gill mechanism, and because of closure of shells. It is of interest, therefore, to determine the temperature at which an animal enters into the hibernating stage and whether or not there is a definite correlation between the shell movements of a mollusk and the temperature of the surrounding water.

Experiments on the effect of temperature upon shell movements of the clam (*V. mercenaria*) were begun on November 17, 1934, and continued until July 29, 1935. They were conducted in a large outdoor concrete tank, 10 by 20 feet, at the laboratory of the U. S. Bureau of Fisheries in Milford, Conn. The tank was so constructed that the water entered it only at the last third of each flood tide and flowed out only partially at the ebb. Thus, the water in the tank was partly renewed twice every twenty-four hours. At low water stages the tank retained approximately 4,000 gallons of water. Because of this arrangement rapid changes in the temperature and salinity of water in the tank were rather uncommon. A roof over the tank protected it from the hot sun

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and heavy rainfalls, facilitating still further the maintenance of a comparatively even temperature and salinity.

Methods

Altogether 399 records from 47 different clams were obtained, each representing the movements of a clam's shell-valves during a 24-hour period. Usually the records of two clams were taken simultaneously. Clams were attached to a recording apparatus for varying periods of time ranging from one to eighteen days. During the course of this work the water temperature in the experimental tank varied from — 1.0°

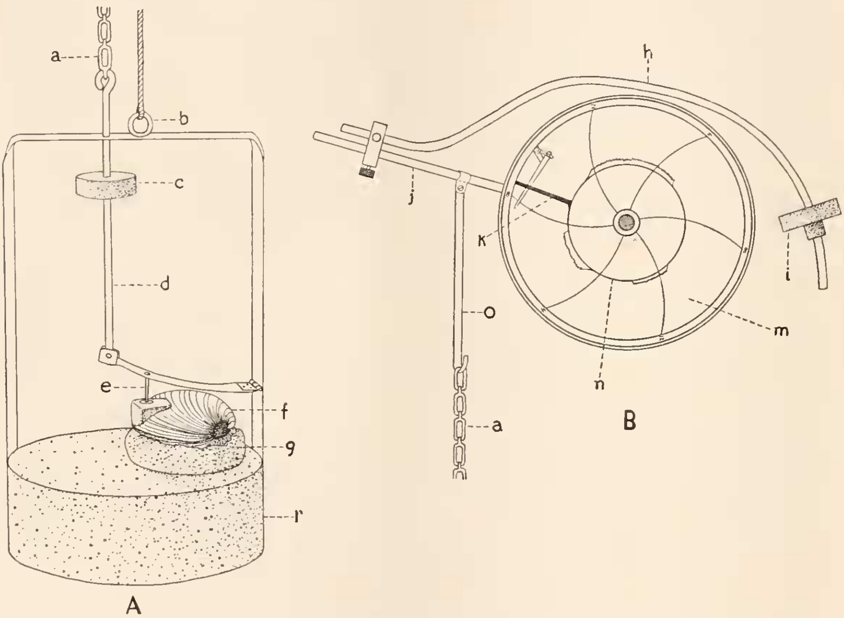

Fig. 1. Apparatus employed in studies of shell movements of clams. Description in text.

to 28.0° C., thus covering almost the entire range of temperature to which clams are subjected under natural conditions. The temperature of the water was recorded continuously by Brown's recording thermometer which was checked frequently against thermometers certified by the U. S. Bureau of Standards.

Each clam was immobilized by imbedding one of its shell-valves in a mixture of sand and cement. The animals were connected to the lever of a recording apparatus in such a way that each movement of the shell was recorded on a chart. The apparatus (Fig. 1) consisted of two main parts, a foundation for keeping an experimental animal in a desired position (*A*), and a Foxboro recorder (*B*). An animal (*f*) imbedded in a block (*g*) of sand-cement mixture was placed on a large round concrete base (*r*) and connected to a recording instrument by a rod (*d*) and a chain (*a*) which was attached to a hook (*o*) of the recording apparatus. A flat piece of cement with a hole in the center was sealed to the free shell-valve of a clam, and on it rested a fine metal pin (*e*). By moving the nut (*i*) along the bent rod (*h*) the weight of a structure connecting the animal to the recording apparatus could be very accurately counterbalanced. This arrangement made it possible to eliminate any unnecessary pressure which would be exerted upon the clam. The rod (*j*) was connected to a writing pen (*k*) which recorded each movement of a clam shell upon the chart. By moving the hook (*o*) along the rod (*j*) the record of valve movement on a chart could be increased or decreased, as desired. In these experiments the distance between the experimental animal and the recorder was about 10 feet. The depth of the water over the clams varied from 4 to 7 feet depending upon the stage of tide.

While the time recorder has already been employed by other investigators in studying the shell movements of mollusks (Galtsoff, 1928), the method of holding the animal in a desired position and attaching it to the recorder, as described in this paper, is a new one.

The main advantage of using the apparatus described here, in preference to those employed by other investigators, is that it considerably simplifies the experimental work by rendering the handling and replacement of animals very easy. By pulling up the cord tied to the ring (*b*) of the foundation unit, the entire lower portion of the apparatus can be quickly raised from the bottom and the animal examined, or new animals substituted for the old ones. All manipulations in placing the animal in position and connecting it to the recording machine are performed out of water. The use of the chain (*a*) eliminates long rods, which were commonly used by other workers.

At each change of chart on the recording apparatus the experimental animal was tapped lightly to compel it to close its valves tightly. After this was achieved, a base line (*n*) was drawn on the chart by rotating it 360°. Having a distinct base line, every movement of a shell, no matter how slight, could be distinguished on the chart (*m*).

Results

Table I and Fig. 2 show the percentage of time the clams remained open at different temperatures. While subjected to very low temperatures (— 1.0° to + 1.9° C.) all the clams remained completely closed.

Altogether 56 records were obtained at such temperatures. At temperatures ranging from 2.0° to 2.9° C., with the exception of one case when an animal was open for about 5 hours, all the clams were inactive. A very slight increase in clam activities was noticed at temperatures ranging from 3.0° to 4.9° C. At the latter temperature the majority of experimental animals remained completely closed, but a few opened on several occasions, bringing the average of open time to 9 per cent. A sudden increase in clam activities was noted at 5.0° to 5.9° C., when the percentage of time open increased to 35 per cent. Such a pronounced increase in shell activities indicates that for many clams the critical hibernating temperature lies somewhere between 5.0° and 6.0° C.

TABLE I

Number of 24-hour records of shell activities obtained at each temperature ranging from −1.0° to 28.0° C., per cent of total time, and average time shells remained open at each temperature during 24-hour period.

Temperature	No. of records	Percentage of total time shells opened	Average time shells opened during 24 hours		Temperature	No. of records	Percentage of total time shells opened	Average time shells opened during 24 hours	
° C.			hours	minutes	° C.			hours	minutes
−1.0– 0.1..	18	—		—	14.0–14.9	8	88	21	7
0.0– 0.9..	8	—		—	15.0–15.9	16	81	19	26
1.0– 1.9..	30	—		—	16.0–16.9	6	78	18	43
2.0– 2.9..	26	1	0	14	17.0–17.9	12	84	20	10
3.0– 3.9..	30	4	0	58	18.0–18.9	6	89	21	22
4.0– 4.9..	32	9	2	10	19.0–19.9	4	76	18	14
5.0– 5.9..	22	35	8	24	20.0–20.9	12	86	20	38
6.0– 6.9..	6	29	6	58	21.0–21.9	6	90	21	36
7.0– 7.9..	12	65	15	36	22.0–22.9	10	86	20	38
8.0– 8.9..	22	67	16	5	23.0–23.9	4	78	18	43
9.0– 9.9..	22	74	17	46	24.0–24.9	16	69	16	34
10.0–10.9..	4	88	21	7	25.0–25.9	9	71	17	2
11.0–11.9..	8	85	20	24	26.0–26.9	6	83	19	55
12.0–12.9..	26	84	20	10	27.0–27.9	4	89	21	22
13.0–13.9..	14	71	17	2					
					Total	399			

At 7.0° to 7.9° C. all the clams were open some of the time, bringing the average time open to 65 per cent. From 8.0° to 10.9° C. a further increase in shell activities was shown. At 10.9° C. the animals remained open 88 per cent of the total time. As the water warmed from 11.0° to 27.9° C. no definite correlation between the temperature of the water and the length of time the shells remained open could be detected. Between these two points, the percentage of open time fluctuated between 69 and 90.

The individual differences displayed by the clams used in these experiments were quite significant. For example, while some of the animals exposed to temperatures of 5.0° to 5.9° C. remained open for the entire period of twenty-four hours, others did not open at all.

At low temperatures the clams may remain completely closed for several days. For example, one clam had its shell closed from noon on December 16, 1934, until noon on January 3, 1935, a period of 18 days. The temperature of the surrounding water during that period fluctuated from — 1.0° to 6.5° C. Another clam remained completely

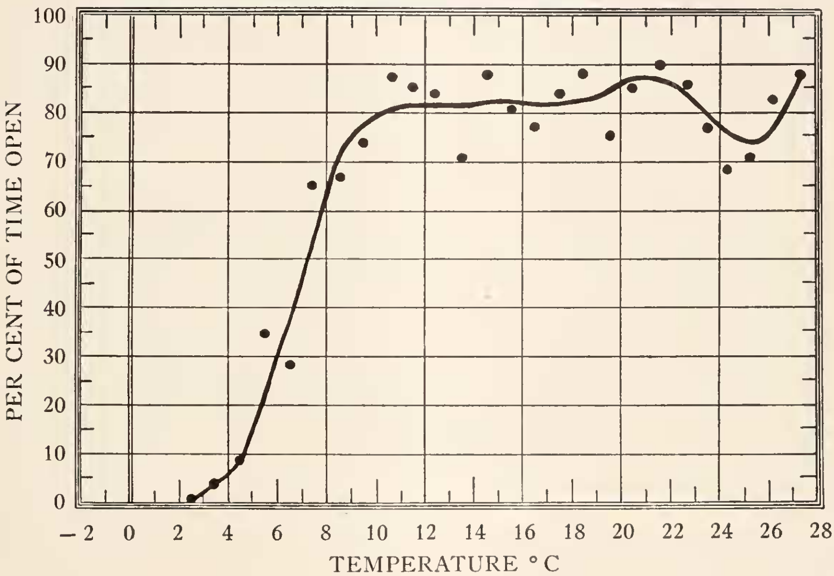

Fig. 2. Percentage of time clams remained open at different temperatures during 24-hour periods.

closed from March 8 to March 19, 1935. In several other instances the animals' shells remained closed for various periods extending from 3 to 6 days. In every one of these cases, the record of shell activity showed no deviation from the base line, thus indicating that not even a slight movement of the shells took place during such a prolonged period. Somewhat similar observations were made by Galtsoff (1928) on one specimen of *O. virginica* which remained tightly closed for 67 hours when left in cold water of a temperature varying from 0.5° to 1.6° C.

Galtsoff (1928), in his work on *O. virginica,* could not find a definite correlation between the effect of temperature and the time the shells of oysters remained open. This was due, probably, to the fact that in his experiments the temperature of the water varied within the comparatively narrow range of 13.0° to 22.0° C. No systematic observations were performed at low temperatures. Similar conclusions could have been reached in this work if the observations had been confined to higher temperatures only. As has been mentioned already, there was no correlation found between the time the clam shells were open and the temperature increase from 11.0° to 27.9° C. If, however, the shell movements are examined at temperatures ranging from 0.0° to 11.0° C., the correlation between the rise in temperature and the gradual increase in duration of openness of the valves is noticed. This is especially evident within the range of 3.9° to 10.9° C., in which the average period of openness increases from 4 to 88 per cent (Fig. 2). Such an increase indicates that as soon as the water temperature gradually rises from the hibernation point to 11.0° C., the factors or conditions controlling the opening of the shells approach the optimum.

The present study, however, does not provide definite information as to the exact temperature at which the optimum conditions for opening of clam shells are reached. Within a 11.0° to 27.9° C. temperature range the shells are open from 69 to 90 per cent of the total time, but the time the shells of the animals remain open does not increase proportionally to the increase in temperature. The highest percentage of time open is recorded at temperatures 21.0° to 22.0° C. when the clams remained open 90 per cent of total time, or 21 hours and 36 minutes per 24-hour period. The average period of time the shells remained open at temperatures from 11.0° to 27.9° C. is 19 hours and 35 minutes. This figure closely resembles those obtained by some other investigators in their studies of oysters. Nelson (1921), basing his conclusions on the records of 3 oysters (*O. virginica*) kept under observation for 21 days, states that the animals remained open an average of 20 hours per day. Galtsoff (1928), from more numerous observations, concluded that the average period of time the shells of oysters remained open is 17 hours and 7 minutes per day. Hopkins (1931), working on *O. lurida,* found that the oysters were open and presumably feeding over 20 hours per day. From the study of the movements of clam shells and from observations of other investigators on oyster shell movements, it appears that under favorable conditions these pelecypods keep their shells open as long as possible.

Experimenting with *O. lurida,* Hopkins (1931) came to the conclusion that it is not so much the existing temperature of the water which determines how long the shells remain open as it is the changes in temperature which occur. This sensitivity of oysters to temperature changes varies in an inverse manner with the temperature of the water. Thus, a small drop in temperature causes closure of the shell if the temperature is well below the optimum, but produces no effect if near the optimum. In clams no such effect of sudden changes in temperature could be detected. For instance, on December 2, 1934, between 2:00 and 3:00 P.M., the water temperature in the experimental tank rose

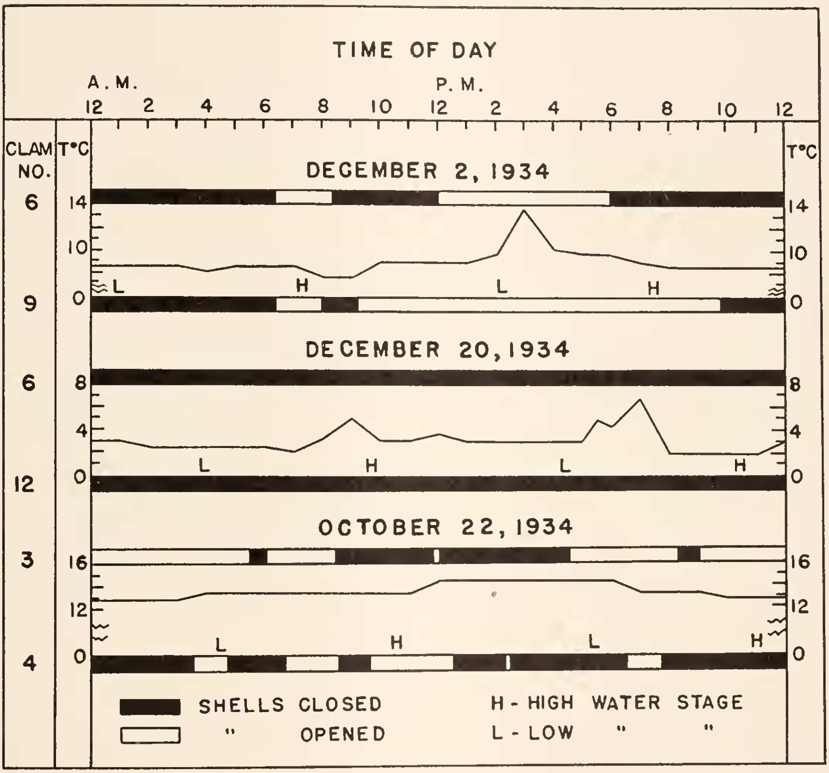

FIG. 3. Records of shell activities of clams and temperature of surrounding water during 24-hour periods. A sudden change in temperature (December 2 and 20, 1934) failed to cause the specimens to exhibit rapid closing or opening of shells. Shells closed and opened when temperature remained unchanged (October 22, 1934). No correlation between the tidal stages and shell movements could be observed. *H*—high-water stage, *L*—low-water stage.

from 9.5° to 13.5° C., and two hours later decreased to 9.5° C. (Fig. 3). Both of the experimental animals, whose shells were open, remained apparently undisturbed. In another case, on December 20, 1934, the water temperature in the experimental tank increased from 3.0° to 6.5° C. within two hours and then quickly dropped to 2.0° C. Neither of the two experimental animals showed any noticeable activities.

It appears that in *Venus mercenaria* the mechanism controlling the opening and closing of the shells is less sensitive to minor temperature changes than that of the oyster. In clams, the closing or opening of the shells is very often performed when the temperature of the surrounding water remains at the same point for some time. On the other hand, the closing or opening often occurred at decreasing temperatures, while again, in numerous other instances, these phenomena took place at increasing temperatures (Fig. 3, October 22, 1934). As far as can be judged by examining hundreds of the records obtained in this work, small changes in the temperature of the surrounding water do not directly influence the shell movements of clams.

During periods of openness the adductor muscles of the clam do not remain in the same position but relax and contract, indicating the changes in tonus level. Contraction of the muscles, although quite pronounced, seldom results in the complete closing of the shells. The data obtained help to answer the question whether there is a definite periodicity in contraction and relaxation of clam muscles, and, if so, whether such periodicity is affected by exposing the animal to different temperatures. Figure 4 represents the records of the shell movements of two experimental animals, Nos. 14 and 16, exposed to different temperatures ranging from about 0.0° to about 20.0° C. and having intervals of about 4.0°. The temperature of the water during these experiments fluctuated not more than ± 1.0° C. Each record represents the activities of the clam for a period of 12 hours, from 6:00 P.M. until 6:00 A.M. The night period is chosen in preference to daytime because the changing of charts in the recording apparatus, usually made in daytime, slightly disturbed the animals. By taking the night half of a daily record, more reliable information is available. The muscles controlling the shells of clams relaxed and contracted, sometimes at very brief, and at other times at prolonged intervals (Fig. 4). It is difficult, however, to find a definite periodicity throughout any of the 12-hour periods shown in Fig. 4. Although during several brief intervals the movements of the shells were of a definitely periodic type and exhibited a rhythmic character, more often they occurred as unsystematic and inconsistent. In this respect the shell activities resemble those of oysters, in which, according to Hopkins (1936), partial closures of the shells are sometimes periodic, sometimes only occasional and unorganized.

Clams whose shell activities are graphically shown in Fig. 4 present an opportunity of comparing the behavior of two individuals subjected to identical environmental conditions. With the exception of the records obtained at the temperature of 16.0° C., all other records of the shell activities of these two clams were obtained simultaneously. At the tem-

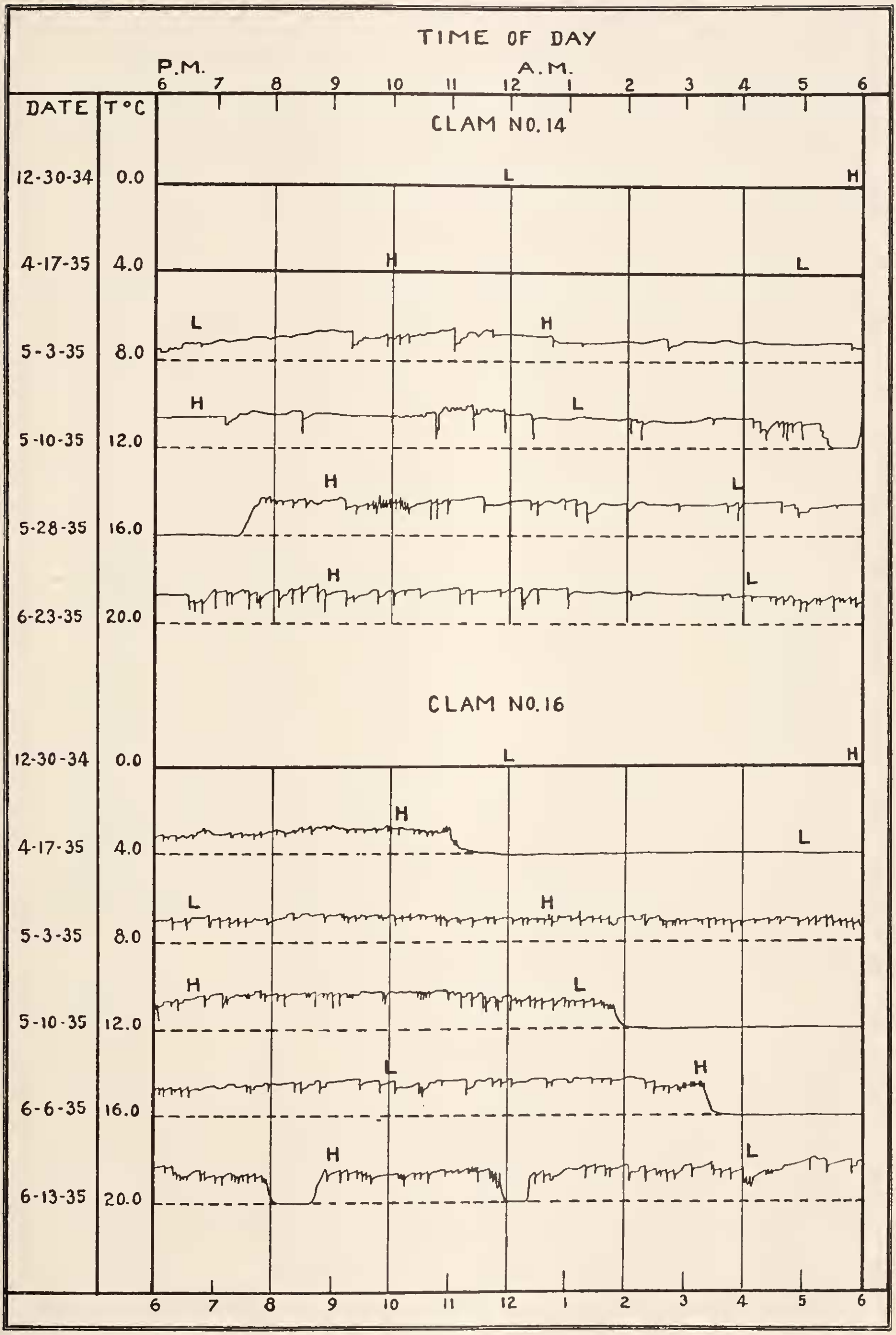

FIG. 4. Records of shell movements of two clams Nos. 14 and 16, exposed for 12-hour periods to different temperatures ranging from 0.0° to 20.0° C. Base line is indicated by series of dots. *H*—high-water stage, *L*—low-water stage.

perature of 0.0° C. both animals remained closed, thus exhibiting uniform behavior. At 4.0° C. one clam remained closed whereas the other was open part of the time. At higher temperatures both clams were active. The records show that there were considerable individual differences in the behavior of these animals although they were subjected to the same external environmental conditions. Such variability may probably be explained as due to internal causes.

In these experiments no definite correlation between the stage of the tide and shell movements of the experimntal animals could be detected. This is demonstrated in Figs. 3 and 4 which show activities of clams at different tidal stages. The failure of the experimental animals to react

Table II

Percentage of time the shells of clams remained closed at daytime and night when exposed to different temperatures.

Temperature classes	Number of records	Number of clams	Average percentage of daylight closed	Average percentage of night closed
0.0– 4.9° C.....	7	3	67.0	74.0
5.0– 9.9° C.....	24	6	36.0	8.0
10.0–14.9° C.....	27	5	20.0	9.0
15.0–19.9° C.....	40	6	18.0	23.0
20.0–24.9° C.....	46	9	23.0	18.0
25.0–28.0° C.....	19	5	23.0	20.0

in a definite way to tidal changes is attributed to the fact that the tanks, where the animals were kept, are so constructed that they are filled at flood tide only and retain part of this water during the ebb stage. Therefore, fluctuations in temperature and salinity of water in the tank were not as great as those in the adjoining harbor.

The material on hand permits the answer to the question whether there is a correlation between opening and closing of clam shells and light and darkness. Nelson (1921) suggested that such correlation does exist for oysters. His conclusions were based upon oysters lying on a natural oyster reef subjected to the usual changes in temperature, salinity, pH and other factors found in open coastal waters. Galtsoff (1928), working in the laboratory under the fairly stable conditions of a relatively constant water supply and lesser differences between diurnal and nocturnal illumination, found no correlation between periods of closure and daylight hours. Webb (1930), working on *O. edulis,* found that the onset and termination of daylight have but little influence on the behavior of oysters as judged by their valve movements. Hopkins

(1931) observed the diurnal variation in the amount of time oysters (*O. lurida*) remained open, but this, according to his opinion, could be directly correlated with temperature fluctuation. In the present study 163 complete (24-hour period) records were examined. All other records showing that the animal was either open or closed for the entire period of 24 hours were not taken into consideration. The period of daylight was taken as the time between sunrise and sunset. After averaging all the data it was found that the clams kept their shells closed during 25 per cent of the total daylight, and 19 per cent of the total time of darkness. Thus, it appears that whereas there was no diurnal variation in shell activities of the clams, the animals were closed for a somewhat longer period in daylight than in darkness.

Records, mentioned above, were obtained between April 10 and July 29, 1935, thus covering the period of 110 days during which the environmental conditions of clam existence were gradually changing. In that span of time the temperature of the water increased from 3.7° to 27.5° C. Such a change in temperature, from below hibernation point for the majority of the clams to the maximum temperature of the year, offered an opportunity to determine whether the ratio between time of shell closure at daylight and at night varied with the rise in temperature as the season progressed. To answer this question all 163 records were arranged in six temperature classes, 5.0° apart. In referring to Table II, which shows the results obtained, it should be remembered that because the number of records is different for each temperature-class the direct comparison between classes is somewhat difficult. However, by studying this table it will be noted that the ratio of time the shells remained closed in daylight or at night varied considerably with the temperature. Such variation is especially significant at the temperature ranging from 5.0° to 14.9° C. At these temperatures the animals had their shells closed for a much longer time in daylight than at night. At present no explanation can be advanced for the occurrence of this phenomenon.

Summary

1. A new apparatus, by means of which the shell activities of many bivalve mollusks can be measured and recorded, is described.

2. The analysis of 399 daily records of shell activities of 47 clams, subjected to temperatures ranging from — 1.0° to 28.0° C., showed that the length of time which the animals remain open partly depends upon the temperature of the surrounding water.

3. For the majority of clams hibernation begins soon after the water temperature decreases to 5.0° and 6.0° C. At lower temperatures the

clams may remain completely closed for very long periods. No shell movements were exhibited, and no disposal of ejecta occurred.

4. Within the temperature range of 3.9° to 10.9° C., the average period of openness increased from 4 to 88 per cent of the total time, showing a correlation with the rise of temperature.

5. There was no correlation between the duration of openness of the clam shells and the temperature increase from 11.0° to 27.9° C. Within this temperature range the shells were open from 69 to 90 per cent of the total time, but the percentage did not increase simultaneously with the increase of water temperature.

6. The highest percentage of time open was recorded at temperatures 21.0° to 22.0° C., when the clams remained open 90 per cent of the total time, or 21 hours and 36 minutes per 24-hour period.

7. Small changes in the temperature of the surrounding water did not influence the shell movements of clams.

8. There appeared to be no definite periodicity in the clam shell movements. During brief intervals, the shell movements may be of a periodic type and exhibit a rhythmic character, but generally they appeared to be unsystematic and inconsistent.

9. There were considerable individual variations in the behavior of clams kept under identical environmental conditions.

10. Under the conditions of the experiments no definite correlation between the stages of tide and the shell movements of the animals could be detected.

11. The animals were closed for somewhat longer periods in daytime than in darkness.

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